

The Mating System and Prey Selection in the Digger Wasp *Aphilanthops hispidus* W. Fox (Hymenoptera: Crabronidae)

JOHN ALCOCK

School of Life Sciences, Arizona State University, Tempe AZ 85287-4501

Abstract.—The mating system of the digger wasp *Aphilanthops hispidus* W. Fox at a site in central Arizona is one in which males patrol the edges of a large nesting/emergence area in a narrow dry watercourse and also around one or more flowering shrubs of catclaw acacia. Patrolling males sometimes pounce on unreceptive females that they encounter in their flight paths suggesting that they may be seeking recently emerged virgin females. After mating, females build nest burrows in the dry wash. They stock their nests primarily with small native bees belonging to five different families. The introduced honey bee, *Apis mellifera*, is however the single most frequently taken prey species. That females of *A. hispidus* also take the occasional wasp demonstrates that they are generalist predators unlike their close relatives, which specialize in the capture of *Formica* ants.

Although widespread in the southwestern United States and northern Mexico, little is known about the digger wasp *Aphilanthops hispidus* W. Fox. Indeed, nothing has been written on the wasp's behavior other than a short note (Evans 1977) that listed the bees taken as prey by one female of the species. Some other members of the genus are known to prey exclusively on ants (Bohart 1966). In addition, the territorial mating system of *A. subfrigidus* has been described in some detail (O'Neill 1990). Here I report on the natural history of *A. hispidus*, a common species in desert habitat near Phoenix, Arizona. The focus of the paper will be on how males attempt to acquire mates and on the identity of the prey species taken by nesting females.

METHODS

Observations on the behavior of male and female *A. hispidus* were made at a desert site about 4 km north of the intersection of East McDowell Road with Power Road (which then becomes the Bush Highway). The site features a dry wash; the wasps were studied at a location about 1 km up the wash to the east of Bush

Highway where the sand and fine gravel bed was only 4 to 6 m wide (Fig. 1). The wash was bordered primarily by creosote bush (*Larrea tridentata* (DC.) Coville), the dominant plant in the area, with occasional foothills paloverdes (*Parkinsonia microphylla* Torr.), ironwood trees (*Olneya tesota* A. Gray), catclaw acacia (*Acacia greggii* A. Gray), and buckhorn cholla cactus (*Opuntia acanthocarpa* (Engelm. & Bigelow) F.M. Knuth).

The wasps were studied over four years: in 2006, from 24 April to 11 May for a total of 9 days; in 2007, from 29 April to 4 May for a total of 4 days; in 2008, from 21 April to 2 May for a total of 5 days; and in 2009, from 7 April to 7 May for a total of 17 days. On any given day, the study site was visited from 1 to 4 h beginning at various times from mid-morning to late afternoon. During the observer's visits, any females that were seen carrying prey and about to enter their nests, many of which were located in a section of wash approximately 240 m in length, were captured and divested of their prey. Collections of prey were subsequently submitted to either Roy Snelling of the Los Angeles County Natural History Museum or John Ascher of the



Fig. 1. A dry wash used as a nesting site by *Aphilanthops hispidus* in the Utery Mountains near Mesa, AZ.

American Museum of Natural History for identification.

To study male behavior, I stood next to plants on the wash border where I could see male wasps flying past. I attempted to capture these individuals in an insect net, and if successful, I marked the captured wasps on the dorsum of the thorax with a DecoColor paint pen before releasing them. All the individuals taken at one spot on the same day initially received the same distinctive color mark (e.g., a red horizontal bar or two white dots). When a marked male was recaptured on the same or subsequent day, it received another color mark that identified it as a particular individual. The mark-recapture data help determine that the males visited a given location over a period of one or more days, a pattern characteristic of patrolling males participating in a scramble competition mating system. In addition, records were made of the reaction of flying males to

perched females and to dead pinned specimens that they encountered in the course of their travels.

RESULTS

*The mating system of *Aphilanthops hispidus*.*—Early in the flight season, large numbers of males were seen flying rapidly and sinuously in and around the outer portions of flowering creosote bush growing along the 240 m section of the wash where females had nested in the previous year (and where they would nest again in the subsequent year). Later in the flight season, when the acacias along the wash began to bloom, patrolling males flew in and around the outer parts of these plants, having largely abandoned their routes around creosote bush by this time. Thus, from 9 to 18 April 2009, large numbers of males traveled past the creosote bush growing by the nesting/emergence area. But when the first acacia began to flower on 18 April (Fig. 2), patrolling males then appeared at this location. As additional plants came into bloom, male wasp activity shifted almost entirely to these locations. By midday 21 April, only two or three males were seen by the creosote bushes where they had been common earlier, whereas dozens of wasps could be found at the several flowering acacias located 330 to 600 m from the lower end of the creosote bush patrolling area. This pattern persisted through 7 May with the wasps continuing to leave plants that had stopped flowering while shifting to those acacias that had more recently come into full flower.

Although on one day, 21 April 2008, large numbers of males were seen and captured in the latter part of the afternoon at the creosote bush site, patrolling males were far more numerous during mid- to late morning during the 2009 flight season (Fig. 3). The many males counted as they flew past an observation point by a shrub during the short (2 min) sample periods during the peak of male activity in 2009 indicates just how abundant patrollers



Fig. 2. The first acacia (*Acacia greggii*) to flower and to attract mate-searching males of *Aphilanthops hispidus* in 2009.

were at these times. The fact that only a small proportion of the marked individuals were recaptured on subsequent days also shows that there was a large pool of males visiting particular shrubs. For example, from 22 to 29 April 2009, a total of 82 unmarked males were captured and marked at a set of three acacias growing within 35 m of one another. On 30 April, 18 of 24 males (25%) taken at these plants were unmarked, suggesting a total population of patrollers in the area in the hundreds.

The occurrence of recaptured males demonstrates that at least some males return to locations at or near where they were initially captured. Indeed, all three males that were marked on 30 April 2009 and then recaptured were each taken three

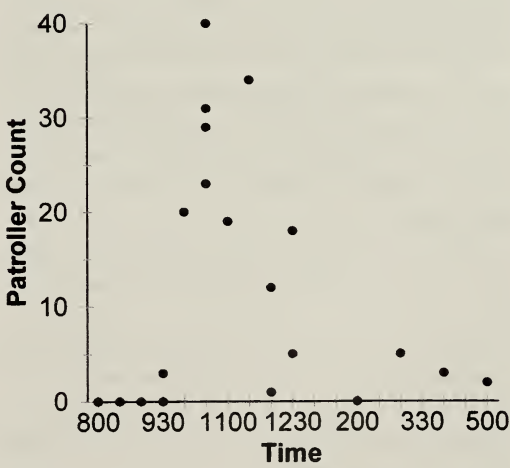


Fig. 3. The number of times a presumptive male of *Aphilanthops hispidus* flew past a fixed point on the exterior of a creosote bush by a nesting/emergence site during a two-min observation period at various times on five days between 9 and 16 April 2009.

times at the same bush in the space of two hours. The three marked males taken on 7 May were recaptured three times each in the space of an hour at a flowering acacia that had not been in full flower on previous visits to the wash but was within 20 m of acacias where patrolling male wasps were seen and taken. Other marked males were also recaptured over a period of two or more days usually at or near the original point of capture (Table 1). The maximum interval between the marking and recapture of any male was six days in 2006, five days in 2007, two days in 2008 and 14 days in 2009 (for two different individuals).

The function of male behavior was revealed when males interrupted their flight forward to zigzag toward females foraging on acacia flowers, where females were commonly seen. A few males made brief contact with the females (N = 7 observations in 2008 and 2009) before resuming their patrol flight. Males also touched pinned, freshly killed females (N = 9 observations), and even attempted copulation, when these females (N = 4) were placed in areas visited by patrolling males. The only naturally occurring mating pair was observed about 1030 M.S.T. on 23 April 2008 as the pair rested in a creosote bush at the edge of the wash in a heavily patrolled corridor (Fig. 4). When the male left his mate, she remained in place for a few minutes and was mounted twice by males that attempted copulation but failed as the female shook herself free on both occasions.

The fact that the vast majority of patrolling males either ignored or merely ap-



Fig. 4. A pair of *Aphilanthops hispidus* perched in a creosote bush along a dry wash that served as a nesting and emergence area for the wasp.

proached dead nesting females pinned to creosote bush or catclaw acacia suggests that odor cues associated with virgin (?) females are usually necessary to elicit complete copulatory attempts. On the other hand, the fact that a few patrollers pounced very briefly on fellow males and even a honey bee in two instances indicates that visual cues play some role in the acquisition of mates.

Prey selection by females of Aphilanthops hispidus.—Once females had mated, they appear to have returned to the emergence area to construct their nests given that every year large numbers of burrows were constructed in the same 240 m-long wash

Table 1. Mark-recapture data for male *Aphilanthops hispidus* at the Usery Mountain study site.

Year	Location	Number marked	Number recaptured on-	
			Same day	Subsequent day
2006	Creosote bush	72	0	5 (7%)
2007	Acacia	73	5 (7%)	7 (10%)
2008	Creosote bush	94	0	3 (3%)
2009	Creosote bush	110	7 (6%)	15 (14%)
2009	Acacia	141	13 (9%)	20 (14%)

segment whose borders were patrolled by males each year. Males were never seen inspecting or harassing nesting females at or near their burrows, and thus females, which probably had mated once soon after emergence, were able to dig their nests and to provision them without interference. Prey-laden females flew to their burrow entrances, even when carrying honey bees almost as large as a wasp itself, and hovered there briefly before plunging into the open entrance. If the prey item failed to slip quickly into the tunnel, the wasp entered, turned about, and dragged the prey into the nest.

Females carried prey against their venter, holding the bee or wasp with their midlegs (Fig. 5). They provisioned the nest primarily with honey bees and native bees (Table 2), although occasionally they utilized small wasps. Five families of bees are represented in the prey list. Nesting in 2009 began at a time when the creosote bushes still had some bee-attracting flowers but by late April and early May, when nest provisioning was still occurring, the local creosote bush had largely completed flowering. At this time, females of *A. hispidus* were regularly seen foraging for nectar on catclaw acacias but they were not seen hunting for prey at these plants.

DISCUSSION

Males of *A. hispidus* appeared to be engaged in a scramble competition for mates with individuals patrolling the borders of a large emergence area from which many virgin females emerge each year. Searching males also flew past flowering acacias known to attract nectar-foraging females. The fact that males often fly upwind close to or within the outer portions of selected plants suggests that they are searching for odor and visual cues associated with receptive females perched in the vegetation. The infrequency with which matings were observed in this study and the lack of interest males showed in provisioning females suggests that females



Fig. 5. A female of *Aphilanthops hispidus* waiting in a creosote bush after having been disturbed as she attempted to enter her nest with prey, a honey bee.

of *A. hispidus* mate just once, as appears to be the typical pattern in crabronid wasps and many other Hymenoptera (Hughes et al. 2008; Paxton 2005; Strassmann 2001). If true for *A. hispidus* as well, then males that reach virgin females first presumably gain a large fitness advantage over their rivals. However, if virgin females only emerge in the first few weeks of the flight season, one would not predict that males would continue to be found patrolling for mates a month after they were first seen, as was the case in 2009. Perhaps some females emerge late in the flight season or perhaps some mate more than once.

Scramble competition for mates has evolved many times in insects (Seidemann 1999; Thornhill and Alcock 1983) and other animals (e.g., Kappeler et al. 2002; Schwagmeyer 1988). This mating system appears to be associated with evenly or unpredictably distributed receptive females coupled with the presence of many competing males. These factors apply to *A. hispidus* at the Usery Mountain site given the large

Table 2. The prey selected by provisioning females of *Aphilanthops hispidus*.

2007	2008	2009
Colletidae		
<i>Colletes circidii</i> Timberlake (4)	<i>Colletes</i> sp. (2)	<i>Colletes</i> sp.
Megachilidae		
<i>Trachusa larreae</i> (Cockerell)	<i>T. larreae</i> (2)	
<i>Megachile odontostoma</i> Cockerell	<i>Megachile</i> sp. (3)	<i>Megachile</i> sp.
<i>Megachile newberryae</i> Cockerell		
<i>Megachile gentilis</i> Cockerell		<i>Anthidium</i> sp.
		<i>Osmia subfasciata</i> Cresson (2)
Andrenidae		
<i>Andrena prunorum</i> Cockerell	<i>Andrena</i> sp.	
	<i>Andrena candida</i> Smith	<i>A. candida</i> (2)
	<i>Andrena fracta</i> Cassad & Cockerell	<i>A. fracta</i> (9)
	<i>Ancylandrena larreae</i> (Timberlake)	<i>A. larreae</i> (2)
Halictidae		
<i>Nomia melanderi</i> Cockerell (2)	<i>Nomia howardi</i> Cockerell	
	<i>Nomia tetrazonta</i> Cockerell	<i>N. tetrazonta</i> (2)
<i>Lasioglossum sisymbrii</i> (Cockerell)	<i>L. sisymbrii</i>	
Apidae		
<i>Diadasia rinconis</i> Cockerell	<i>Anthophora</i> sp. (3)	
	<i>A. californica</i> Cresson	
	<i>Nomada</i> sp.	
	<i>Ericrocis lata</i> (Cresson)	<i>E. lata</i>
		<i>Melissodes paroselae</i> Cockerell
		<i>Epeolus</i> sp.
		<i>Habropoda pallida</i> (Timberlake)
<i>Apis mellifera</i> Linnaeus	<i>A. mellifera</i> (26)	<i>A. mellifera</i> (16)

number of nests scattered more or less evenly over a long segment of wash from which many virgin females and males emerge during the flight season. Any male that attempted to defend a territory would be in possession of only a small fraction of a plant where the probability that a virgin female would arrive was no greater than elsewhere. Moreover, the territorial individual would constantly have to respond to passing males, whose entry into his defended space would be costly to prevent.

The scramble competition mating system of *A. hispidus* differs markedly from the mating system of its congener, *A. subfrigidus* (O'Neill 1990). Males of that species defend small display territories close to those of several other males. The males' territories are clustered in areas where *Formica* ant alates are swarming. Each

individual at the lek appears to mark his site with an attractant pheromone while chasing and even grappling with any fellow males that enter his territory. Receptive females may visit these sites to select a partner from among those present, although mating has not been observed in this species.

Males of *A. subfrigidus* possess paired hairbrushes along the outer portion of the lower margin of the clypeus that they appear to use to mark vegetation in their territories with pheromones from glands in the head in the manner of their relatives in the genus *Philanthus* (Evans and O'Neill 1988). The fact that males of *A. hispidus* also possess clypeal brushes of about the same size as those of *A. subfrigidus* (Kevin O'Neill, personal communication) raises the possibility that some males under some

circumstances may engage in scent marking in an alternative mating system yet to be observed in this species.

The ecology of *A. subfrigidus* is similar but not identical to that of *A. hispidus* (O'Neill 1990). Females of *A. subfrigidus* do form nesting aggregations but these are small with many fewer individuals than present at the Usery Mountain *A. hispidus* site. The smaller number of nesting females in populations of *A. subfrigidus* must translate into fewer adult males, which in turn could make the costs of male territoriality less for this species, and thus more likely to evolve. In addition, by placing their display territories within ant swarm sites, males of *A. subfrigidus* may be taking advantage of the attraction of the prey resource for females of their species. Much still remains to be learned, however, about why lek territoriality evolves in some species while related ones exhibit scramble competition polygyny (Thornhill and Alcock 1983).

Prey selection by Aphilanthops hispidus.—Females of *A. hispidus* are generalist predators that take a wide variety of solitary bees, as well as the introduced honey bee, which was by far the most commonly captured prey species at this study site over the years. Interestingly, Evans found native bees belonging to four families in a cache of seven individuals within an excavated nest (Evans 1977), suggesting that individual wasps do not specialize on one or a few of the prey species available to them. Females of *A. hispidus* also take the occasional wasp but were not observed with ants, the sole prey of the well-studied *A. frigidus* (Evans 1962, 1970) and *A. subfrigidus* (Bohart 1966; O'Neill 1990). It seems likely that females of *A. hispidus* exploit any bees of suitable size, especially those that visit creosote bush for nectar or pollen. Thirteen of the species on the prey list from the Userys (Table 2) also appear on the list of native bees collected at one or more of 47 *Larrea* sites studied by Minckley et al. (1999). In addition, seven wasps were taken from

provisioning females in three years (2007–2009), including a vespid, *Parancistrocerus toltecus* (de Saussure), another eumenine and five other wasps that have unfortunately been misplaced.

With respect to prey selection, *A. hispidus* is more similar to the generalist bee and wasp predators in the genus *Philanthus* than it is to others in its own genus, which apparently take only ants (alate queens of *Formica* in the case of *A. frigidus* and *A. subfrigidus*) as is also true for wasps in the closely related philanthine genus *Clypeadon*, although these species hunt worker ants rather than reproductives (see review in Evans and O'Neill (1988)).

ACKNOWLEDGMENTS

I am grateful to Kevin O'Neill for his instructive review of the manuscript and his willingness to examine specimens of *A. hispidus* to see if males possess clypeal hairbrushes. Bill Rubink also helped improve the manuscript. Thanks to John Ascher for identifying two samples of prey taken by females of *A. hispidus*. For the first batch of prey, I called on Roy Snelling to help, which he did with his characteristic professionalism and generosity. I dedicate this paper to the memory of Roy Snelling.

LITERATURE CITED

- Bohart, R. M. 1966. A review of *Aphilanthops* and related genera (Hymenoptera: Sphecidae). *Proceedings of the Entomological Society of Washington* 68: 158–167.
- Evans, H. E. 1962. A review of the nesting behaviour of digger wasps of the genus *Aphilanthops*, with special attention to the mechanism of prey carriage. *Behaviour* 19: 239–260.
- . 1970. Ecological-behavioral studies of the wasps of Jackson Hole, Wyoming. *Bulletin of the Museum of Comparative Zoology* 140: 451–511.
- . 1977. *Aphilanthops hispidus* as a predator of bees (Hymenoptera: Sphecidae). *Pan-Pacific Entomologist* 53: 123.
- and K. M. O'Neill. 1988. *The Natural History and Behavior of North American Beewolves*. Cornell University Press, Ithaca, N.Y. 278 pp.
- Hughes, W. O. H., B. P. Oldroyd, M. Beekman, and F. L. W. Ratnieks. 2008. Ancestral monogamy shows kin selection is key to evolution of sociality. *Science* 320: 1213–1216.
- Kappeler, P. M., B. Wimmer, D. Zinner, and D. Tautz. 2002. The hidden matrilineal structure of a solitary lemur: implications for primate social

- evolution. *Proceedings of the Royal Society of London B* 1502: 1755–1763.
- Minckley, R. L., J. H. Cane, L. J. Kervin, and T. H. Roulston. 1999. Spatial predictability and resource specialization of bees (Hymenoptera: Apoidea) at a superabundant, widespread resource. *Biological Journal of the Linnean Society* 67: 119–147.
- O'Neill, K. M. 1990. Female nesting behavior and male territoriality in *Aphilanthops subfrigidus* Dunning (Hymenoptera, Sphecidae). *Pan-Pacific Entomologist* 66: 19–23.
- Paxton, R. J. 2005. Male mating behaviour and mating systems of bees: an overview. *Apidologie* 36: 145–156.
- Schwagmeyer, P. L. 1988. Scramble-competition polygyny in an asocial mammal: Male mobility and mating success. *American Naturalist* 131: 885–892.
- Seidemann, K. 1999. The race for females: The mating system of the red mason bee, *Osmia rufa* (L.) (Hymenoptera : Megachilidae). *Journal of Insect Behavior* 12: 13–25.
- Strassmann, J. E. 2001. The rarity of multiple mating by females in the social Hymenoptera. *Insectes Sociaux* 48: 1–13.
- Thornhill, R. and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, MA. 547 pp.